Demographic Processes Influencing Population Viability of the Iowa Pleistocene snail (Discus macclintocki)

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ABSTRACT.—Understanding the importance of variable local population abundance and the limited potential for dispersal and genetic exchange is crucial for the conservation of many species with limited geographic distribution and specialized habitat requirements. Because of rarity, it is often difficult to study the relative importance of variation in recruitment and survival and their net effect on population growth. We designed a survey of natural populations of endangered Iowa Pleistocene snails (*Discus macclintocki*) using the robust mark-recapture design to estimate population size and vital rates. A dense population remained stationary throughout the 6-y study whereas vital rates fluctuated substantially in two much smaller populations. In the smaller populations rates of growth varied from sharply increasing to sharply decreasing among years, and changes in estimated recruitment were the primary vital rate influencing these fluctuations. Snails were highly sedentary and sampling at random locations showed that the populations were highly subdivided within a site. Fluctuations in demographic rates and patchy distribution may provide the basis for substantially different rates of genetic change within and among sites. Although in the short-term, fluctuations in recruitment of these snails may influence local dynamics most substantially, long-term threats of habitat loss or climatic change will likely affect survival of adults and persistence of the populations.

INTRODUCTION

The Iowa Pleistocene snail (*Discus macclintocki* F.C. Baker, Discidae) is a state and federally endangered land snail that occurs on a specialized habitat type termed an algific talus slope in the karst topography region of northeastern Iowa and adjacent Wisconsin, Minnesota and Illinois. The region, often referred to as the ''driftless area,'' escaped the last glacial advances leaving the Paleozoic-age bedrock subject to erosion (Prior, 1991). Algific slopes, usually north facing, occur where air circulates over underground ice producing a constant stream of cold moist air through vents on to the slope. These vents are typically covered with a loose talus layer and thin plant and litter cover. Many rare plant and animal species that are considered glacial relicts persist only on these small areas of suitable habitat (U.S. Fish and Wildlife Service, 1984). Sites generally vary in size from 0.2–4 ha, although some sites are more extensive. Many sites are protected through ownership or easement by conservation organizations including the U.S. Fish and Wildlife Service, Iowa Department

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of Natural Resources and The Nature Conservancy, but some sites are on private land. Currently 24 of 37 sites in Iowa and Illinois where the Iowa Pleistocene snail occurs are protected by some form of conservation protection. Frest (1987) conducted extensive study of the species during the 1980s and his reports formed the basis for the species recovery plan (U.S. Fish and Wildlife Service, 1984) that guides current conservation.

The Iowa Pleistocene snail is a classic example of an endangered species with a limited geographic range, very specific habitat requirements, limited potential for dispersal and genetic exchange and variable local population abundance. Although there has been substantial interest in population and evolutionary ecology of terrestrial snails, there have been relatively few detailed studies of density, dispersal and other demographic vital rates (Williamson *et al.*, 1977; Cowie, 1984; Baur, 1986; Sherley *et al.*, 1998; Backeljau *et al.*, 2001).

In general, conservation biologists agree that there is a practical need for understanding the interaction of demographic and genetic factors in extinction processes (Lehmkuhl, 1984; Lande and Barrowclough, 1987; Nunney and Campbell, 1993; Young and Clarke, 2000). Although in a theoretical sense there is some controversy about the relative importance of genetic factors and demography in determining the minimum viable sizes of wild populations (Lande, 1988; Spielman *et al.*, 2004), in practical terms demographic fluctuations will often be of immediate concern. Furthermore, when population dynamics of endangered species are studied, the emphasis is often placed on the number of individuals in a population, on single elements of a species life history or in projecting the potential persistence of the population (Boyce, 1992). Less attention is paid to estimating the integrated demographic vital statistics that ultimately determine population growth and viability (White, 2000; Williams *et al.*, 2002). Unfortunately, estimating abundance and vital rates of most endangered species is complicated by the fact that they are limited in distribution, obviously not abundant, and often subject to strict regulation regarding disturbance and handling. Furthermore, without continued monitoring it is difficult to distinguish yearly variation in population size from long-term demographic trends.

We had an opportunity to use mark-recapture methods applied over 6 y to estimate vital demographic parameters of Iowa Pleistocene snails (Henry *et al.*, 2003). Our objectives were to use current mark-recapture theory and methods to estimate population size, and to directly estimate finite population growth rate and its component demographic parameters of survival and recruitment (Nichols *et al.*, 2000). We also related these vital rates to other life history characteristics of the population including movement and spatial variation in abundance.

METHODS

Data collection.—Between 2001 and 2006 we sampled populations of Iowa Pleistocene snails at eight algific slope sites in Clayton, Dubuque, Fayette and Jackson counties, Iowa. Ostlie (1992) originally noted that snails could be efficiently sampled by placing unfinished wooden boards on the site to which the snails would readily attach. We designed a double-sampling monitoring scheme based on sampling five boards (0.124 m^2, ~20 × 61 cm) initially placed at random locations across the site combined with intensive mark-recapture sampling at a cluster of eight adjacent boards (0.991 m^2) (Henry *et al.*, 2003). Using the boards increased the probability of capture, compared with grab samples and other approaches used by previous researchers (Frest, 1987; Anderson, 2000). A 5.1 cm grid on the underside of boards enabled us to record snail locations and estimate local movement. We checked mark-recapture boards for five consecutive days after placement and then boards were removed from the site. Each year, sampling of all sites was completed during a 6-wk period from mid-May through late Jun., which is the most active period for this snail

species (Ostlie, 1992). Although the coordinates of the sampling boards were the same each year, all boards were removed after sampling to prevent damage to sites and to avoid providing artificial habitat for snails. Juvenile snails, <5 mm, were marked with individual color combinations of paint. Adult snails, ≥5 mm, were marked with colored, numbered bee (BetterBee) or fish tags (VI alpha fish tags, Northwest Marine Technology) attached with superglue, or sometimes with unique paint combinations. We used a different color at each site in each year so we could distinguish marked cohorts. Previous research (Ostlie, 1992) and our own observations indicated that tag loss was minimal. Shell diameter, shell height, umbilicus diameter and number of whorls were measured with a caliper to the nearest 0.5 mm on each snail according to the methods of Pilsbry (1939). We recorded air temperature, humidity and soil temperature at each mark recapture location to evaluate whether environmental covariates affected snail capture probabilities.

We report detailed mark-recapture data from three sites where we sampled for all 6 y. Site 98 is in Clayton County, Iowa and is owned by The Nature Conservancy. It is a relatively stable, but steep slope with an open canopy and loose talus layer with fern cover at many sampling locations. The algific features at Site 281, a privately owned site in Fayette County, Iowa, extend into a pasture with several large cold vent areas covered by loose talus and also containing fern cover. Cattle were excluded from Site 281 in 2001. Site 207 is owned by the U.S. Fish and Wildlife Service in Dubuque County, Iowa. It is a large, stable slope with large boulders and rock outcroppings, ferns and typical deciduous forest cover. Snails were captured at these sites from 2001 through 2006. We also report less detailed data from monitoring the randomly located boards at other sites when such data are relevant to questions about population trends. We documented all sampling times and locations, complete with photo points in Henry *et al.* (2003).

Estimating demographic parameters.—We designed the mark-recapture sampling to take advantage of the robust design (Pollock, 1982; Kendall *et al.*, 1997) that uses a combination of closed and open population models to estimate demographic parameters. Effectively, the design estimates abundance (N_i) for each year of the study ($i = 1,6$), assuming population closure during 5-d sampling periods (Williams *et al.*, 2002) as implemented in program MARK (Cooch and White, 2006). A major advantage of the robust design is that data from the five-d sampling periods is used to assess variation in capture probability, enabling robust estimation of N_i and the vital rates of change between years.

After establishing the recapture structure of the data, we estimated the open-model parameters between years using the models of Pradel (1996; Nichols *et al.*, 2000) that enable estimation of apparent survival (Φ_i), per capita recruitment (f_i), seniority (γ_i) and finite population growth rate (λ_i). These models have now been extended to the robust design framework (Cooch and White, 2006) and not only allow for time variation in capture probability, but also heterogeneity among groups of individuals (Pledger, 2000). In the case of Iowa Pleistocene snails, recruitment is defined as the number of new snails < 5 mm at year *i* per snail of all size classes in the population at year *i*-1. Recruitment combines the effects of reproduction, growth and immigration. The seniority parameter is the probability that a snail present at year $i + 1$ was already present in the population at year *i*. Survival, recruitment, seniority and population growth rate are not all uniquely identifiable in a single analysis because they are related by $\lambda_i = \phi_i + f_i = \phi_i/\gamma_{i+1}$ (Nichols *et al.*, 2000). Given this relationship, seniority (γ_{i+1}) can be interpreted as the proportional sensitivity of finite population growth rate (λ_i) to changes in survival (Φ_i), enabling us to assess whether changes in survival or recruitment contributed more to population growth or decline (Nichols *et al.*, 2000).

We began open population modeling with the basic Cormack-Jolly-Seber (CJS) structure by fitting models in the Link-Barker formulation (Schwarz and Arnason, 2006), computing a variance inflation factor ($\hat{c}$) that was used to adjust reported standard errors. Although strictly speaking the CJS structure is not the global model for all the complex data types we analyzed, it is an important point to start with goodness-of-fit tests before selecting among models using Akaike's Information Criterion (AIC, Burnham and Anderson, 1998). We fit models in which parameters were allowed to vary among years (denoted i) and then fit simpler models in which some or all parameters were constant (denoted by a dot). We selected among models using $QAIC_c$, AIC adjusted for both small sample size and extra-binomial variation (Burnham and Anderson, 1998).

We used analysis of variance, with a repeated measures error structure, to assess spatial and temporal variation in the numbers captured and the observed percentage immature snails captured at random locations within and among sites. We weighted counts by the number of days between visits, which varied from 2 to 5 d. We concentrated the statistical testing on whether the abundance or percentage immature was variable among sites and locations within sites.

<center>RESULTS</center>

Estimates of vital rates.—We captured and recaptured the most snails at site 281 (Table 1), where we observed some of the individual snails in 4 of the 6 y of the survey. Fewer individuals were captured at sites 98 and 207, but we made sufficient recaptures at all these sites to test goodness of fit and to select appropriate models.

Data from site 281 fit the CJS model ($\chi^2 = 25.21$, np = 16, $\hat{c} = 1.58$). However, models with time-specific recapture probability and survival in both the primary and secondary capture periods were unnecessarily complex ($\Delta QAIC_c > 18$). A Pradel lambda model that used the robust design formulation with closed captures and a two-group heterogeneous mixture of capture probabilities (program MARK, White and Burnham, 1999) with constant lambda (λ.) and survival (Φ.) fit the data best ($QAIC_c = 776.98$, np = 24). A model with year-specific growth rate (λ_i) and constant survival (Φ.) did not fit as well ($\Delta QAIC_c = 4.47$) nor did the model with λ. and Φ_i ($\Delta QAIC_c = 4.49$). Under the best model, constant λ. = 1.00 (95% CI, 0.84–1.00) and constant Φ. = 0.38 (95% CI, 0.30–0.46) (Table 1). The estimated population at the mark-recapture sampling location on site 281 remained essentially constant. Under the Pradel recruitment model (Cooch and White, 2005) constant seniority γ. = 0.38 (Table 1).

Judged by $\hat{c}$, there was slight, but not severe, evidence of extra-binomial variation (Burnham and Anderson, 1998) ($\chi^2 = 56.96$, np = 16, $\hat{c} = 3.56$) in the data from site 98. A Pradel lambda model that used the robust design formulation with closed captures and a two-group heterogeneous mixture of capture probabilities with year-specific growth rate (λ_i) and survival (Φ_i) fit the data best ($QAIC_c = 357.84$). A model with constant λ. and Φ. (same structure as best model for site 281) fit much worse ($\Delta QAIC_c = 40.05$), and a model with year-specific growth rate (λ_i) and constant survival (Φ.) also was not a competitive alternative ($\Delta QAIC_c = 11.55$). Under the best model, estimated λ_i ranged from 3.78 in 2001 to 0.00 in 2004, whereas estimated Φ_i ranged from 0.05 to 1.00 (Table 1). The estimated population at the mark-recapture sampling location on site 98 increased initially then declined steadily after 2002 (Table 1, Fig. 1). Under the alternative formulation of the Pradel model, recruitment (f_i) varied from 3.37 in 2001 to essentially 0.0 in 2004 and only in 2004 was $\gamma_i > 0.5$.

Data from site 207 also could not be readily fit with a simple CJS model and like site 98 there was evidence of extra-binomial variation ($\chi^2 = 94.23$, np = 16, $\hat{c} = 5.89$). A Pradel

TABLE 1.—Snails captured (M_{t+1}), capture probability (p_i), estimated population (N_i), finite population growth rate (λ_i), apparent survival (Φ_i), per capita recruitment (f_i) and seniority (γ_i) of Iowa Pleistocene snail populations recaptured on 0.991 m^2 sample locations on three algific sites in northeastern Iowa, 2001–2006

Site and Parameter	2001		2002		2003		2004		2005		2006	
Site 281												
M_{t+1}	142		172		180		172		88		91	
p_i[a]	0.30	(0.10)[b]	0.19	(0.05)	0.21	(0.08)	0.07	(0.01)	0.30	(0.09)	0.32	(0.08)
N_i	579	(162)	576	(123)	578	(97)	581	(84)	577	(132)	575	(162)
$\lambda.$	1.00	(0.08)										
$\Phi.$	0.38	(0.04)										
$f.$	0.62											
$\gamma.$			0.38									
Site 98												
M_{t+1}	28		86		8		20		1		5	
p_i	0.16	(0.04)	0.13	(0.02)	0.04	(0.02)	0.19	(0.05)	0.19	(0.12)	0.29	(0.12)
N_i	48	(11)	173	(26)	44	(25)	30	(6)	1	(0.02)	6	(2)
λ_i	3.78	(1.16)	0.37	(0.15)	0.51	(0.20)	0.00	(0.00)	ne[c]	ne	ne	
Φ_i	0.06	(0.06)	0.10	(0.04)	0.82	(0.28)	1.00	(0.00)	0.05	(0.05)	ne	
f_i	3.37	(1.05)	0.07	(0.06)	0.42	(0.47)	0.00	(0.00)	0.13	(0.09)	ne	
γ_{i+1}			0.02	(0.02)	0.60	(0.27)	0.65	(0.26)	1.00	(0.00)	0.26	(0.23)
Site 207												
M_{t+1}	16		4		11		29		17		26	
p_i	0.21	(0.06)	0.05	(0.06)	0.33	(0.08)	(0.29)	(0.05)	0.25	(0.06)	0.15	(0.04)
N_i	22	(5)	18	(23)	12	(2)	35	(4)	22	(4)	45	(11)
λ_i	0.96	(1.16)	0.58	(0.72)	2.79	(1.00)	0.67	(0.20)	1.90	(0.64)	ne	
Φ_i	0.19	(0.25)	0.16	(0.17)	0.21	(0.14)	0.20	(0.08)	0.62	(0.23)	ne	
f_i	0.76	(1.03)	0.43	(0.67)	2.58	(0.98)	0.48	(0.18)	1.28	(0.55)	ne	
γ_{i+1}			0.20	(0.22)	0.27	(0.35)	0.08	(0.05)	0.30	(0.12)	0.33	(0.11)

[a] Probability of capture of the larger group in the mixture

[b] Standard error of the estimate

[c] Not estimated under the model

lambda model that used the robust design formulation with closed captures and a two-group heterogeneous mixture of capture probabilities with year-specific growth rate (λ_i) and constant survival ($\Phi.$) fit the data best ($QAIC_c = 604.88$). A model with constant $\lambda.$ and $\Phi.$ did not fit the data as well ($\Delta QAIC_c = 5.83$), nor did a model with year-specific growth rate (λ_i) and survival (Φ_i) ($\Delta QAIC_c = 6.25$). Under the best model estimated λ_i ranged from 2.79 in 2003 to 0.58 in 2002, and estimates were more variable than other sites because of lower recaptures (Table 1). Although variable among years, the estimated population at the mark-recapture sampling location on site 207 fluctuated less than that at site 98. At site 207 the population appeared to be increasing somewhat at the end of the survey (Table 1, Fig. 1). Under the alternative formulations of the Pradel model, recruitment (f_i) varied from 2.58 in 2003 to 0.43 in 2002 and no value of $\gamma_i > 0.5$.

Although snails are not completely sessile, the data and modeling support the suggestion that horizontal movement was minimal within the algific site habitat. Based on the recaptures during the 5-d recapture surveys, the maximum horizontal displacement of snails ranged from about 11 cm (SE = 6.4, n = 14) at site 98 to as much as 23 cm (SE = 5.6, n = 71)
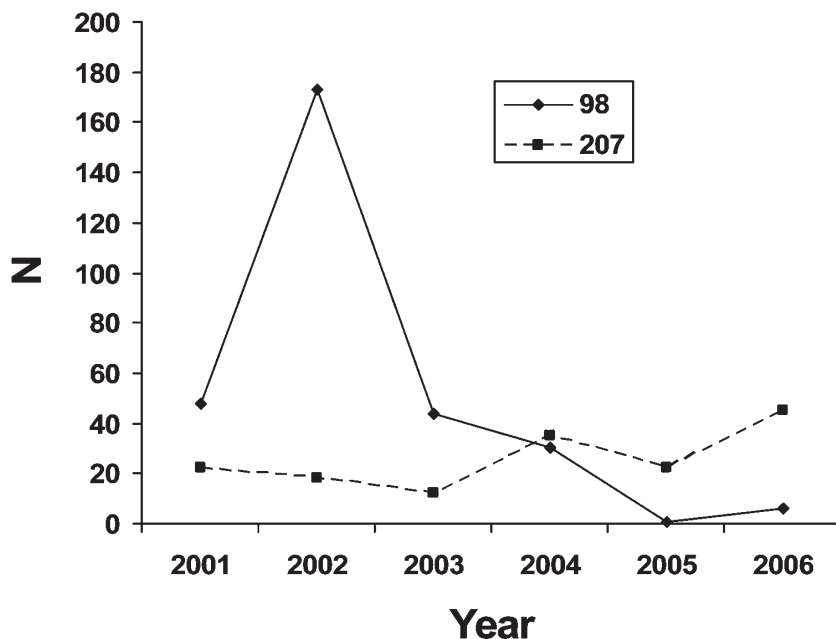
FIG. 1.—Estimated population size (N_i) of Iowa Pleistocene snails recaptured on 0.991 m^2 sample locations on 2 algific sites in northeastern Iowa, 2001–2006

at site 281. The distribution of movements is highly skewed with most snails recaptured <10 cm from the original location (Henry *et al.*, 2003). The fact that the boards were removed each year and we subsequently recaptured individuals for multiple years within the same grid location at a site, further supports the idea that most snails remain within the same square-meter area between years. This observation is entirely consistent with previous study, which suggests that most movement is vertical within the talus (U.S. Fish and Wildlife Service, 1984; Ostlie, 1992; Wallendorf and Clark, 1992).

We estimated that if snails moved in a straight line at the observed rate for an entire year an individual might move as far as 16.7 m, a distance that is within the algific slope habitat of most sites (Henry *et al.*, 2003). We recaptured a snail in 2004 on site 281 that had moved 18 m since the time it was marked the previous year. Based on these movement data we concluded that we could assume geographic closure within years and validly convert population estimates to density. Average density among years at the recapture sample locations was 26 snails/m^2 on site 207, 51 snails/m^2 on site 98, and 583 snails/m^2 on site 281.

Captures at random-board locations.—The number of snails captured at random locations was a function of the differences among sites (F = 2.59, df = 7, 32, P = 0.031) and locations within the sites (F = 3.14, df = 32, 179, P < 0.001), but the pattern among the repeated years was not different (F = 1.70, df = 5, 179, P = 0.137) (Table 2). Humidity at the time of sampling influenced captures (F = 2.37, df = 5, 179, P = 0.041), but air temperature (F = 1.48, df = 5, 179, P = 0.197) and soil temperature (F = 1.11, df = 5, 179, P = 0.358) did not. The proportion of five random locations at which ≥2 snails were captured each year at a board was greater at the sites where the mean number of snails captured on these random boards was above the median (Table 2), indicating less spatiotemporal variation within these sites.

TABLE 2.—Mean number of snails, percentage of locations where ≥2 snails were captured each year, and percentage immature snails captured under 0.124 m² boards placed at random locations on algific slopes in northeastern Iowa, 2001–2006

Site	Mean number captured	SE	Percent of locations with ≥2 snails captured each year	Percent immature	SE
281	5.92	0.77	100	7.73	3.35
98	1.06	0.73	60	4.62	3.17
207	0.27	0.84	20	0.00	
33	1.48	0.76	40	4.32	3.31
62	0.32	0.92	60	2.00	3.98
99	2.13	0.74	100	8.50	3.19
137	3.29	0.78	60	13.88	3.38
297	5.04	1.05	80	14.44	4.57

An identical analysis to that for number of captures, showed that the percentage immature snails captured at random locations was also a function of differences among sites (F = 2.35, df = 7, 32, P = 0.047), and locations within the sites (F = 1.58, df = 32, 179, P = 0.032) (Table 2). We captured the largest percentages of immature snails at sites 137 and 297, however the percentage of immature snails varied more among locations within site 137 compared with 297. The percentage of immature snails was more spatiotemporally consistent at locations within site 281 where estimated density was largest.

Size structure.—The analyses regarding the variation in immature snails are reinforced by the size distribution of snails captured on random boards. Combined data from eight sites indicate predominance (86%) of mature individuals (shell diameter ≥ 5 mm) (Fig. 2).

We captured a consistently wide range of differently-sized snails on site 281 (Fig. 2). The population at site 281 had snails in every size class and a larger number of snails measuring 6 and 7 mm. The size distribution observed at site 98 indicates a population with little recruitment of immature snails (Fig. 2). In fact, 90% of the snails on site 98 were 7 or 8 mm in size. The size distribution on site 207 was more variable among years than the other sites that we intensively sampled (Fig. 2).

DISCUSSION

Our demographic analyses showed that finite population growth rate was constant and equal to 1.0 at site 281 where the population density was greatest. At site 281 seniority was estimated to be constant ($\gamma = 0.38$) and per capita recruitment was also constant ($f = 0.62$) indicating that recruitment was more important to maintaining the constant population than survival (Nichols *et al.*, 2000). These demographic results are supported by the wide range of size classes and presence of a greater than average number of immature snails captured at this site.

In contrast, two other sites (98 and 207) where the population density was an order of magnitude lower than at site 281, finite population growth fluctuated substantially among years. At site 98, recruitment (f_i) fluctuated from well above 1.0 to essentially 0.0, especially in recent years. The estimated population peaked in 2002 and has declined since that time. Although it may be presumptuous to extrapolate this trend (Boyce, 1992), these results suggest a trajectory toward local extinction. In contrast, at site 207 where average density was lowest, the population data suggested a population fluctuating around a constant mean population size rather than exhibiting a distinct decline. No estimate of seniority (γ_i) was
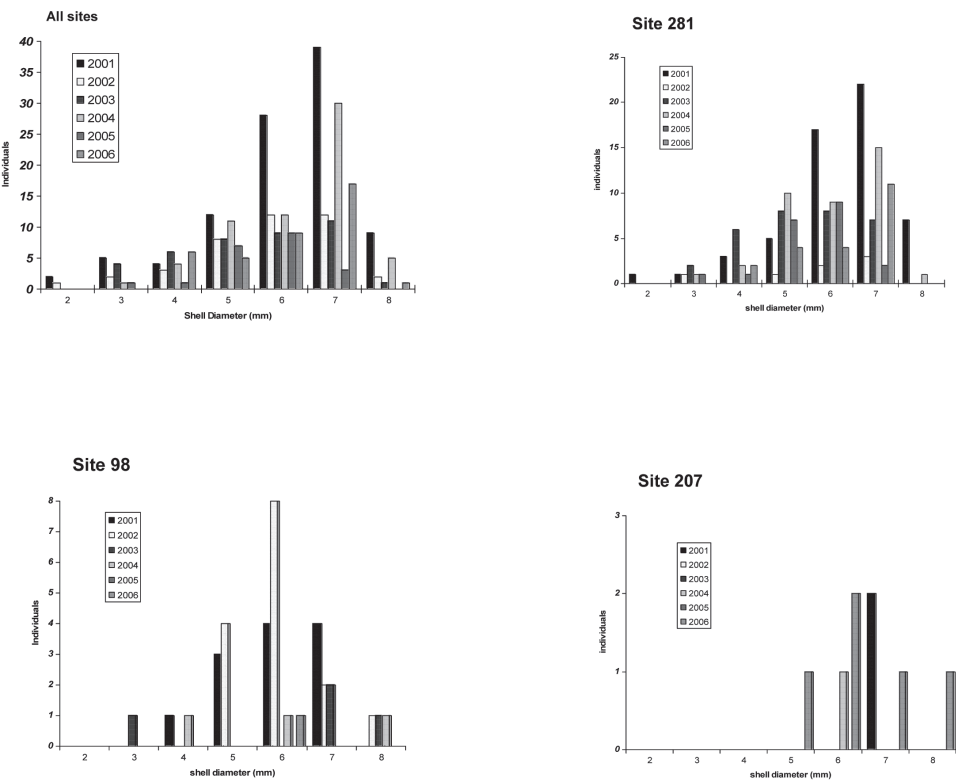
FIG. 2.—Distribution of shell sizes of Iowa Pleistocene snails recaptured at all eight algific sample sites and the mark-recapture sites in northeastern Iowa, 2001–2006

greater than 0.5, suggesting that variable recruitment (f_i) was much more influential than survival (Φ_i) in determining population growth at site 207.

Species recovery plans (U.S. Fish and Wildlife Service, 1984) require knowledge of population abundance as well as estimation of trends. In the case of Iowa Pleistocene snails these results and those of others (Wallendorf and Clark, 1992; Anderson, 2000) show that there are substantial populations within all of these sites but that perhaps not all localized populations are stationary. The estimation procedures based on the robust design produced repeatable and precise estimates of population size at the mark-recapture locations. Methods based on grab samples (Frest, 1987; Anderson, 2000) have much lower recapture probabilities and, therefore, would be expected to have greater bias and decreased precision (Williams *et al.*, 2002). Models assuming closure, such as those of Chao's time and heterogeneity model (Williams *et al.*, 2002), are a substantial improvement over simple counts or estimates based on *ad hoc* methods. But given that our goal was to study demographic trends over multiple years, the robust design Pradel models (Cooch and White, 2006) made the most complete use of the available recapture data.

In the case of the Iowa Pleistocene snail, the monitoring of population trend that is required under a species recovery plan is complicated because of the small size of these snails and their habit of moving vertically through the litter layer. In addition, the algific slopes are fragile because of their steepness and loose rock covering. Activity on a site can dislodge rocks

and soil, compact surface vents and crush snails. Therefore, monitoring methods need to be minimally intrusive and yet be able to reliably detect snails. Although a double-sampling approach (Phillipi *et al.*, 2001; Henry *et al.*, 2003) helps to account for some of the biases, the results presented herein suggest that spatiotemporal variation will make it difficult to derive precise estimates under the assumptions of such sampling approaches.

Suitable habitat for Iowa Pleistocene snails has not been adequately studied (Frest, 1987; Anderson, 2000), but visual inspection clearly indicates that it is not uniform within a site. By monitoring random locations on the site we determined that most of the variation in abundance is associated with differences among sites, although variation within sites was also important. Perhaps not surprisingly, the sites with the fewest number of snails also exhibited the greatest spatio-temporal variation in abundance at a location. Because our results and those previously (Wallendorf and Clark, 1992; Anderson, 2000) show that snails are highly sedentary, it means that the population is highly subdivided within many sites. It follows that comparing density estimates among studies or extrapolating total numbers within a site is problematic (Anderson, 2000; Henry *et al.*, 2003). Anderson (2000) attempted to extrapolate estimates to suitable habitat, although it was unclear to us how she quantitatively defined suitable habitat. To make comparisons, we conservatively calculated density from the area Anderson (2000) sampled and compared it to our estimated average density on the two sites where we both sampled. On site 207 we estimated 26 snails/m^2 where she estimated 11.8 snails/m^2 and we estimated 51 snails/m^2 on site 98 where she estimated 114 snails/m^2 (Anderson, 2000). Recall that our estimate of abundance at the mark-recapture location on site 98 was relatively great when we began shortly after Anderson (2000) completed her studies, but after peaking in 2002 abundance there then steadily declined. In contrast, it appears that snail abundance at site 207 has remained relatively low, but without significant decline, for the last decade despite fluctuations in the estimated demographic rates.

Although these populations of snails exhibited a relatively high survival for small terrestrial gastropods, the analyses indicate that variable recruitment accounts for much of the variation in population growth rates. Frest (1987) studied Pleistocene snails in the laboratory and estimated that it required 2 to 2.5 y for snails to reach maturity. We consistently began capturing snails when they had reached about 4–5 mm (*see* Fig. 2) when they were likely to be about three y old. From the mark-recapture surveys on slope 281 we estimated that once captured, the expectancy of further life averaged an additional 1 to 1.25 y. Combining our observations with those of Frest implies that many captured individuals in this population were alive for at least four y. In fact, we had one adult snail that was recaptured four of the six y that we sampled. This rough estimate of life span would still place the Iowa Pleistocene snail among those considered to have a comparatively short life span among terrestrial gastropods (Heller, 2001). Longevity has important consequences for population persistence. In long-lived species, populations can persist even when recruitment is effectively zero because in a given year minimum $\lambda_i = \Phi_i$ (Nichols *et al.*, 2000). As long as the unique microclimate of the algific slopes is maintained, adult snails will survive and the fluctuations in population rate of change will likely be determined more by variation in recruitment rate.

Unfortunately, very little is known about the reproductive life history of these snails (U.S. Fish and Wildlife Service, 1984; Heller, 2001). Fluctuations in recruitment might be a function of immediate threats to local habitat conditions, such as grazing or trampling on the sites, that would reduce plant cover and litter that is important as both food and cover. In contrast, factors such as global climate change that has been predicted to cause shifts in distribution and abundance in biological communities (Parmesan and Yohe, 2003), could affect the unique microclimate of the sites and have long-term effects on adult survival and population

persistence. Damage from flooding that removes much of the talus layer, leaves sites that are steep and unstable, and directly removes individuals is a catastrophic loss of habitat and snails from which populations cannot demographically recover (Henry *et al.*, 2003). Superficially, site 98 which has substantial fern and moss cover, looks like it is much better snail habitat than site 281, which was previously grazed (Henry *et al.*, 2003). But population levels on site 281 were an order of magnitude larger than those at site 98, suggesting that indirect inferences about potential population levels based on habitat assessment and site history may not provide a completely defendable basis for species conservation.

The demographic analyses support the previously-expressed view that genetic diversity remains relatively high in these snail populations (Ross, 1999) because they exist in numerous local demes with relatively low migration rates, both within sites and especially among sites. Most terrestrial pulmonates are simultaneous hermaphrodites and most breed by cross-fertilization (Heller, 2001). Although the reproductive mode of *Discus macclintocki* is unknown, some stylommatophorans have developed the ability to self-fertilize (Heller, 2001), a life-history trait that would be highly adaptive when populations decline and the chances for cross-fertilization decrease. Reduction in population size may be a major force that reinforces local genetic drift helping to maintain the genetic differentiation observed in other gastropod populations (Viard *et al.*, 1997; Backeljau *et al.*, 2001). Differences in the demographic rates like those that we observed may provide the basis for substantially different rates of evolutionary change within and among sites occupied by *D. macclintocki*. Although in the short-term, fluctuations in recruitment may influence local dynamics most substantially, long-term threats of habitat loss or climatic change will ultimately affect survival and adaptation of adults and persistence of the populations.

LITERATURE CITED

ANDERSON, T. K. 2000. Population size estimates for the endangered Iowa Pleistocene snail, *Discus macclintocki* Baker. *J. Iowa Acad. Sci.*, **107**:34–41.

BACKELJAU, T., A. BAUR AND B. BAUR. 2001. Population and conservation genetics, p. 383–412. *In:* G. M. Barker (ed.). The biology of terrestrial molluscs. CAB International, London.

BAUR, B. 1986. Patterns of dispersion, density and dispersal in alpine populations of the land snail *Arianta arbustorum* (L.) (Helicidae). *Holarct. Ecol.*, **9**:117–125.

BOYCE, M. S. 1992. Population viability analysis. *Ann. Rev. Ecol. Syst.*, **23**:481–506.

BURNHAM, K. P. AND D. R. ANDERSON. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York.

COOCH, E. AND G. C. WHITE. 2006. Program MARK: a gentle introduction. 5th Edition. Cornell University, Ithaca. (http://www.phidot.org/software/mark/docs/book/).

COWIE, R. H. 1984. Density, dispersal and neighborhood size in the land snail *Theba pisana. Heredity*, **52**:391–401.

FREST, T. J. 1987. Final report. Iowa Pleistocene snail project, 1987. Project E-17. Report to the Department of Natural Resources, Des Moines, Iowa.

HENRY, C., W. R. CLARK, M. J. BURNS AND C. L. DETTMAN. 2003. Population monitoring protocol for the Iowa Pleistocene snail (*Discus macclintocki*). U.S. Fish and Wildlife Service, McGregor, Iowa.

HELLER, J. 2001. Life history strategies, p. 413–445. *In:* G. M. Barker (ed.). The biology of terrestrial molluscs. CAB International, London.

KENDALL, W. L., J. D. NICHOLS AND J. E. HINES. 1997. Estimating temporary emigration using capture-recapture data with Pollock's robust design. *Ecology*, **78**:563–578.

LANDE, R. 1988. Genetics and demography in biological conservation. *Science*, **241**:1455–1460.

——— AND G. F. BARROWCLOUGH. 1987. Effective population size, genetic variation, and their use in population management, p. 87–123. *In:* M. E. Soulé (ed.). Viable populations for conservation. Cambridge University Press, Cambridge.

LEHMKUHL, J. F. 1984. Determining size and dispersion of minimum viable populations for land management planning and species conservation. *Environ. Manage.*, **8**:167–176.

NICHOLS, J. D., J. E. HINES, J. D. LEBRETON AND R. PRADEL. 2000. Estimating of contributions to population growth: a reverse-time capture-recapture approach. *Ecology*, **81**:3362–3376.

NUNNEY, L. AND K. A. CAMPBELL. 1993. Assessing minimum viable population size: demography meets population genetics. *Trends Ecol. Evol.*, **8**:234–239.

OSTLIE, W. R. 1992. A monitoring methodology for the Iowa Pleistocene snail (*Discus macclintocki*): 1992 field season. The Nature Conservancy, Iowa Field Office. 24 p.

PARMESAN, C. AND G. YOHE. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**:37–42.

PHILIPPI, T. E., B. COLLINS, S. GUISTI AND P. M. DIXON. 2001. A multistage approach to population monitoring for rare plant populations. *Nat. Areas J.*, **21**:111–116.

PLEDGER, S. 2000. Unified maximum likelihood estimates for closed capture-recapture models using mixtures. *Biometrics*, **56**:434–442.

POLLOCK, K. H. 1982. A capture-recapture design robust to unequal probability of capture. *J. Wildl. Manage.*, **46**:757–760.

PRADEL, R. 1996. Utilization of capture-mark-recapture for the study of recruitment and population growth rate. *Biometrics*, **52**:703–709.

PRIOR, J. C. 1991. Landforms of Iowa. University of Iowa Press, Iowa City. 153 p.

ROSS, T. K. 1999. Phylogeography and conservation genetics of the Iowa Pleistocene snail. *Mol. Ecol.*, **8**:1363–1373.

SCHWARZ, C. J. AND A. N. ARNASON. 2006. Jolly-Seber models in MARK. Chapter 14 in E. Cooch and G. C. White editors. Program MARK: a gentle introduction. 5th Edition. Cornell University, Ithaca. (http://www.phidot.org/software/mark/docs/book/).

SHERLEY, G. H., I. A. N. STRINGER, G. R. PARRISH AND I. FLUX. 1998. Demography of two landsnail populations (*Placostylus ambagiosus*, Pulmonata: Bulimulidae) in relation to predator control in the far north of New Zealand. *Biol. Conserv.*, **84**:83–88.

U.S. FISH AND WILDLIFE SERVICE. 1984. National recovery plan for Iowa pleistocene snail (*Discus macclintocki* (Baker)). U.S. Fish and Wildlife Service, Minneapolis, Minnesota.

VIARD, F., F. JUSTY AND P. JARNE. 1997. The influence of self-fertilization and population dynamics on the genetic structure of subdivided populations: a case study using microsatellite markers in the freshwater snail *Bulinus truncatus*. *Evolution*, **51**:1518–1528.

WALLENDORF, M. J. AND W. R. CLARK. 1992. Evaluation of a population monitoring methodology for *Discus macclintocki*: 1992 field season. Final report to The Nature Conservancy, Des Moines. 28 p.

WHITE, G. C. 2000. Population viability analysis: data requirements and essential analyses, p. 288–331. *In:* L. Boitani and T. K. Fuller (eds.). Research techniques in animal ecology: controversies and consequences. Columbia University Press, New York.

——— AND K. P. BURNHAM. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study*, **46 Supplement**:120–138.

WILLIAMS, B. K., J. D. NICHOLS AND M. J. CONROY. 2002. Analysis and management of animal populations. Academic Press, San Diego.

WILLIAMSON, P., R. A. D. CAMERON AND M. A. CARTER. 1977. Population dynamics of the land snail *Cepaea nemoralis* L.: a six year study. *J. Anim. Ecol.*, **46**:181–194.

YOUNG, A. G. AND G. M. CLARKE (eds.). Genetics, demography, and viability of fragmented populations. Cambridge University Press, Cambridge.